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STUDIES IN THE HIPPOCASTANACEAE, IV. HYBRIDIZATION IN AESCULUS

JAMES W. HARDIN

The topic of hybridization is of prime importance in the study of the genus Aesculus, for much of the confusion concerning the concept of species and the problem of identification of the buckeyes in eastern North America has been due to the mongrel forms so often encountered in the natural populations and gardens. As early as 1869, Loudon stated:

". . . the truth is, that the different kinds of Aesculus and Pavia cross-fecundate so freely, and seedlings vary so much, that there is no limit to the number of varieties that might be produced. The great error (because it creates so much confusion in the nomenclature) consists in giving these varieties to the world as species."

Hybridization in the buckeyes involves only five of the fifteen species: Aesculus hippocastanum, and the four species of Aesculus section Pavia (glabra, octandra, sylvatica and pavia). Aesculus parryi of Baja California and A. californica of California are each geographically isolated and have not been found to hybridize, even under cultivation. Aesculus parviflora of Georgia and Alabama grows with A. pavia and A. sylvatica but does not hybridize with either. Its flowering period is two to four weeks later than either that of A. pavia or A. sylvatica, which apparently would serve as an effective seasonal or temporal isolation barrier. On the other hand, the fact that A. paviflora belongs to a different and distantly related section of the genus from A. pavia and A. sylvatica may explain the complete barrier to hybridization.

The only intersectional hybrid is A. carnea Hayne, which is an allopolyploid (n = 40) resulting from the cross between A. hippocastanum and A. pavia. Aesculus plantierensis André is a sterile backcross (n = 30) between A. carnea and A. hippocastanum. Both of these are garden hybrids and have been studied cytologically by Skovsted (1929) and Upcott (1936).

Many hybrids involving the sympatric species of section Pavia have been recognized, described, and given specific epithets. Both the hybrids arising under cultivation and the forms found

in the natural populations will be discussed.

Many of the hybrids which have been given names represent forms which have arisen in various botanical gardens of Europe and America. Of the six possible hybrid combinations between the four species in section Pavia, all but two, A. octandra × sylvatica and A. glabra × sylvatica, have been previously described in the literature. The latter is still to be identified and there is no reason why it should not appear in cultivation.

Some hybrids involving three parental species have been given names. The exact crosses involved are unknown but it is possible occasionally to identify the parent species to which the hybrid is most nearly referable on the basis of all characteristics.

Johnson (1939) lists many of these cultivated hybrids, with short notes concerning their place of origin. It should be understood that in almost every case the parents of these hybrids have been determined from a study of comparative morphology. Although this is a sound criterion and there has been additional circumstantial evidence from the gardens as to the identity of the parents, none of the crosses was actually made experimentally. The significance of these hybrids arising under cultivation is that they match perfectly the putative hybrids found in the field, and therefore serve more or less as test crosses.

Since F₁ hybrids are not commonly used in horticulture, and none forms a distinct population in nature, formulae instead of specific epithets are used in all cases. The binomials would become especially confusing since introgression is so prevalent, as indicated below.

Intermediate forms between species are often encountered in the field as well as in herbaria, and the interpretation of these intermediate forms is sometimes difficult. The major question

is just what the intermediate forms mean. They may be the result of introgression between distinct species, or an ancestral gene pool in which sympatric speciation is going on at the present time. Anderson (1953) has described a number of tests by which the distinction can be made between introgression and the gene pool hypothesis. The significant points in these five tests which indicate introgression are: 1) the loose association of variables characteristic of the variation pattern in artificially produced hybrids and backcrosses; 2) the introgressants found in the floristically newer or disturbed areas; 3) sterility, if any, showing up in the intermediates; 4) ability to predict, by the method of extrapolated correlates, the introgressing species; and 5) the similarity of experimental hybrids and backcrosses with the putative hybrids found in the field. In accordance with these five criteria, it is concluded that the intermediate forms found in Aesculus populations are the result of sympatric introgression. Much of the evidence in favor of this conclusion has been derived from the analysis of populations using the techniques developed by Anderson. Additional evidence is the high percentage of abortive pollen found in the intermediate forms, the similarity with hybrids arising in cultivation, and the prevalence of hybrids in disturbed habitats.

For an analysis of introgression in the buckeyes, I took random samples of twenty to fifty specimens each, from over thirty populations throughout the range of section *Pavia*. Each specimen consisted of a twig with a mature inflorescence and at least three or four leaves, and was selected from a mature part of the tree or shrub. In every case the entire population was briefly surveyed to obtain an idea of size and the habitat differences; following this the specimens were taken from along a transect through the population, and more or less equally spaced so that the specimens represented the entire length of the transect. Since the shrubby species are occasionally clonal by root sprouts, the spacing was necessary to eliminate the possibility of collecting more than one specimen from each clone.

The analysis of populations of "pure species," hybrid swarms, and those in which hybridization was suspected, was made by the use of pictorialized scatter diagrams as described by Anderson (1949, 1953). After determining the characters to use in this

analysis, the diagrams or graphs were plotted and grouped according to the species crosses. Each of these crosses will be discussed individually. The explanations of the symbols used for the characters are given with the diagrams.

During the preparation of the systematic treatment of the *Hippocastanaceae* in America, about 5000 herbarium specimens were examined and annotated. A word of explanation is in order concerning the method of annotating the hybrid forms. Since introgression is widespread in the populations of eastern United States, it is rare that a specimen taken from a wild population is exactly intermediate between two species, i. e., the F₁ hybrid. Hybrids are more likely to represent backcrosses or various other recombinants. Usually such a backcross or recombinant can be referred to the parental species to which it is most nearly referable on the basis of all characters.

The specimens most nearly intermediate and which could not be placed with one or the other parent were annotated as "species A" × "species B"—the names in alphabetical order. The back-crosses and recombinants were annotated as "species A" (× "species B"), indicating that the specimen was most nearly referable to "species A" (which was probably the backcross parent), and that "species B" contributed the gene minority. There is some objection to this way of annotation, but as yet no other entirely satisfactory system has been proposed.

The citation of specimens is limited here to only one per county.

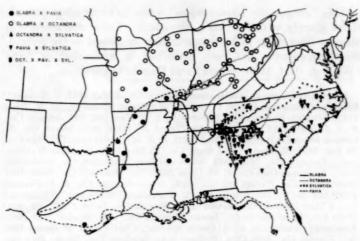
Aesculus glabra × octandra

Aesculus marylandica Booth ex Kirchner, in Petzold and Kirchner, Arb. Muscav. 168. 1864.

Aesculus glabra forma marylandica Koehner ex Schelle, in Beissner et al., Handb. Laubh.-Ben. 322. 1903.

Intermediates between A. glabra and A. octandra may be recognized by their exserted stamens, stipitate glands on the pedicel and perianth surfaces, greater differences between upper and lateral petals than are found in A. glabra, and the irregularity of spines on the ovary wall.

A few F₁ hybrids have been found; most of the intermediates, however, represent backcrosses or various recombinants. Since intermediates are detected by floral characteristics only, some



Map 1. Distribution of hybrids in relation to the ranges of the species.

sterile specimens annotated and cited as A. glabra may actually be A. glabra (\times octandra), which is very common north of the Ohio River, as shown in Map 1.

Aesculus \times arnoldiana Sarg. (Jour. Arn. Arb. 5: 42. 1924.), occasionally cultivated in North America and Europe, represents a cross between A. glabra and the hybrid of A. octandra and pavia, or at least contains the characteristics of these three species, with A. glabra as the most apparent. According to Sargent this arose in the Arnold Arboretum about 1900.

One very interesting feature in the hybrids between A. glabra and A. octandra is the nature of the spines on the ovary wall. The effect of crossing a spiny-fruited type (A. glabra) with a smooth type (A. octandra) does not always result in the entire ovary being either spiny or smooth, or intermediate, but rather there is an unusual mosaic of spines on the wall—an irregularity which appears like sectorial chimeras in the pericarp. Particularly in the F_1 hybrids, only one side on the immature ovary wall will have the stipitate glands (which develop into the spines on the pericarp), or one single row of glands from top to bottom, or a number of small glandular sections separated by smooth areas over the wall.

This "irregularity phenomenon" seems to occur when parents differ sharply in one or more characters. These characters will then be irregularly and asymmetrically expressed in the hybrid. Such irregularity has been described in a number of ferns (Wagner, 1954, 1956; Wagner and Hagenah, 1954).

Specimens examined.—Alabama: Madison Co., 8 May 1881, C. Mohr (A) Illinois: Champaign Co., F. C. Gates 1508.1 (MICH); Coles Co., G. N. Jones 11143 (NY, UC); Hancock Co., 1 May 1844, L. B. Mead (MO, NY); Johnson Co., E. J. Palmer 14971 (A, US); LaSalle Co., J. W. Huett (GH); Macon Co., A. Gleason 281 (GH); Peoria Co., May 1890, F. E. McDonald (UC); St. Clair Co., 29 Apr. 1897, H. Eggert (NY); Stark Co., 15 May 1898, Virginius H. Chase (мо); Tazewell Co., May 1889, McDonald (GH); Vermilion Co., Gates 1463 (US). Indiana: Cass Co., C. C. Deam 19381 (A); Dearborn Co., Deam 5691 (MO); Grant Co., Hardin 673 (GA, MICH, NCSC); Howard Co., R. C. Friesner 15066 (GH, MO, NY, UC); Monroe Co., M. E. Springer 789 (GA, TEX); Tippecanoe Co., 3 May 1912, L. O. Overholts (MO); Warrick Co., Deam 27087 (GH, YY); Wells Co., Deam 758 (NY). Iowa: Madison Co., Ada Hayden 7145 (MO). Kentucky: Bullitt Co., P. A. Davies 249 (GH); Clark Co., R. E. Horsey 1034 (A); Fayette Co., Apr. 1834, R. Peter (GH); Madison Co., Horsey 1072 (A). Michigan: Lenawee Co., Hardin 675 (GA, GH, MICH, NCSC). Missouri: Boone Co., F. Drouet 1901 (GH); Greene Co., Hardin 667 (GA, GH, MICH, NCSC); Marion Co., J. Davis 1462 (A, UC); Jackson Co., Bush 125 (A, GH, NY, US); Jefferson Co., 18 Apr. 1869, Eggert (NY, US); St. Clair Co., Bush 13276 (A, MO); St. Louis Co., Hardin 670 (GA, GH, MICH, NCSC); Taney Co., Bush 4517 (A, MO). Ohio: Ashland Co., Hardin 695 (GA, GH, MICH, NCSC); Belmont Co., Hardin 690 (GA, GH, MICH, NCSC); Crawford Co., 14 May 1897, Kellerman (os); Cuyahoga Co., May 1895, G. B. Ashcraft (NY); Fairfield Co., Horsey 217 (A); Franklin Co., Horsey 224 (A); Hamilton Co., C. G. Lloyd 491 (MICH, US); Harrison Co., Hardin 694 (GA, GH, MICH, NCSC); Logan Co., 9 May 1902, Kellerman (os); Lorain Co., 21 May 1904, F. O. Grover (os); Lucas Co., Horsey 563 (A); Mercer Co., 12 May 1906, S. E. Horlacher (os); Miami Co., 5 May 1883, H. A. Young (вн); Morrow Co., 20 Jul 1901, Kellerman (ов); Perry Co., Apr 1941, F. Clean (os); Richland Co., Horsey 475 (A); Sandusky Co., 2 Jun 1881, R. P. Hayes (os); Vinton Co., 10 May 1901, Kellerman (os); Wyandot Co., 10 May 1901, T. A. Bonser (08). Tennessee: Franklin Co., 5 May 1898, Eggert (MO, NY); Rutherford Co., Sharp et al. 11493 (TENN); Stewart Co., A. W. Jobe 1823 (TENN).

The population in Vinton County, Ohio (Fig. 1) represents "pure" A. octandra, with the variation in size of flowers probably due to environmental conditions. The collections were made from large trees growing along a slope in a mixed mesophytic forest. Collections from Belmont County, Ohio, were taken from scattered trees and shrubs along a stream, through an open pasture, and to the edge of a beech-maple-buckeye woods, which had been lumbered recently. The population shown in Fig. 2 represents trees of A. octandra, with some influence from

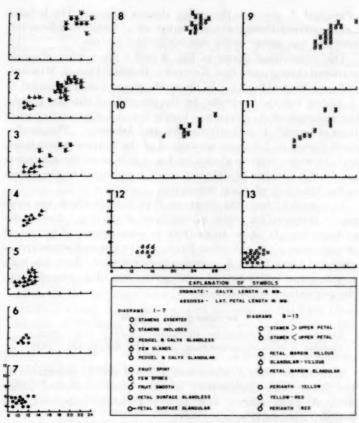


Fig. 1-7. Pictorialized scatter diagrams showing introgression between A. glabra and A. octandra. 1, A. octandra (Vinton Co., Ohio: Hardin 680). 2, A. glabra × octandra (Belmont Co., Ohio: H. 690, 691). 3, A. glabra × octandra (Belmont Co., Ohio: H. 692). 4, A. glabra (× octandra) (St. Louis Co., Mo.; H. 670). 5, A. glabra (× octandra) (Lenawee Co., Mich.; H. 675). 6, A. glabra (Guernsey Co., Ohio; H. 693). 7, A. glabra (Ark. and Mo.; H. 614, 616, 632, 639, 651). Fig. 8-13. Introgression between glabra and A. paria. 8, A. paria (Bowie Co., Texas; H. 570). 9, A. paria (Tallahatchie Co., Miss.; H. 199). 10, A. paria (× glabra) (Holmes Co., Miss.; H. 466). 11, A. paria (× glabra) (Bossier Par., La.; H. 507). 12, A. glabra (× paria) (Polk Co., Ark.; H. 598). 13, A. glabra (Ark. and Mo.; H. 597, 614, 616, 632, 639, 651).

A. glabra, and then shrubs along the creek which are A. glabra with introgression from A. octandra. Figure 3 is similar and represents a population in which A. octandra was found on the

ridges and A. glabra in the valley along a stream. The hybrids were scattered throughout the entire area, which had been cut over and was partly under cultivation and pasture.

The populations shown in Fig. 4 and 5 are typical of many scattered throughout Ohio, Kentucky, Indiana, Illinois, Missouri, and into Iowa (Map 1). In these, the specimens are referred to A. glabra, but they indicate, by the presence of stipitate glands, the influence of A. octandra. Figure 6 and 7 represent populations of "pure" A. glabra from Ohio and Arkanass. The smaller sized flowers in Arkansas are typical of the western populations, and the wide variation shown by Fig. 7 is because the specimens are from a number of different small populations in the region rather than a single local population.

It is evident from the diagrams that hybrids which are most nearly intermediate occur in the zone of overlap between the two species. In these areas there is some degree of reciprocal introgression. On the other hand, northward and westward in glaciated areas where A. octandra does not exist, there has been a widespread infiltration of some germplasm of A. octandra into the populations of A. glabra.

Aesculus glabra × pavia

Aesculus × bushii Schneider, Ill. Handb. Laubh. 2: 251. 1912. Aesculus × mississippiensis Sarg., Jour. Arn. Arb. 2: 120. 1920

Hybrids between A. glabra and A. pavia may be recognized by the flower color (yellow-red), stamens usually exserted, petals unequal, petal margin and surface glandular-pubescent, and pericarp irregularly spiny.

Intermediate forms due to hybridization are found, although infrequently, mostly in the region of overlap between ranges of the two parental species (Map 1), in northern Alabama, east-central Mississippi, Louisiana, southeastern Texas (A. glabra var. arguta × pavia), Arkansas, southeastern Oklahoma and eastern Missouri. There are outlying stations for A. glabra in east-central Mississippi which account for the presence of hybrids in this region.

SPECIMENS EXAMINED.—Alabama: Jackson Co., Harbison 1061 (NCU). Arkansas: Hempstead Co., Bush 1098 (A); Marion Co., D. M. Moore 516 (UARK); Polk Co., Hardin 598 (CA, GH, MICH, NCSC); Stone Co., 26 Apr 1928,

Ashe (NCU). Louisiana: Bossier Par., Hardin 507 (GA, GH, MICH, NCSC). Mississippi: Holmes Co., Hardin 466 (GA, GH, MICH, NCSC); Noxubee Co., Harbison 1061 (A, NCU); Oktibbeha Co., Harbison 1055 (A). Missouri: Bollinger Co., Steyermark 28404 (NY, US); Phelps Co., B. H. Slavin 235 (A). Oklahoma: McCurtain Co., 14 Apr 1940, C. G. Ward (GA). Texas: Jackson Co., S. G. Drushel 10512 (A).

Analyses of populations showing introgression between A. glabra and A. pavia are illustrated in Figs. 8–13. Reciprocal introgression between these two species is apparently restricted, for there is very little detectable influence on either parental species away from the area of the original crosses (Map 1). Figures 8 and 9 indicate populations of A. pavia in Texas and Mississippi. The Mississippi population (Fig. 9) is variable with respect to flower size, probably due to ecological conditions. The plants were growing in mixed hardwoods on the steep slopes of the loess hills and were under varying light conditions. The two populations shown in Figs. 10 and 11 are considered as A. pavia, but with slight introgression from A. glabra evidenced by the variation in color and glandular condition of the perianth. Both populations were in disturbed areas along county roads, and on the Coastal Plain which is the typical habitat for A. pavia.

In Polk County, Arkansas, and on the edge of Big Fork Creek just east of the town of Big Fork, there were a few trees which looked like A. glabra, but the flowers were reddish and had a few glands on the petal margins (Fig. 12). These show practically no variation among themselves, and may possibly represent a number of F₁ hybrids or backcrosses with A. glabra. Aesculus glabra was common throughout the area and along the creek; no A. pavia was found in the region. To give an indication of A. glabra in this series of scatter diagrams, populations from Arkansas have been graphed in Fig. 13.

Aesculus octandra × sylvatica

Aesculus glaucescens Sarg., Trees and Shrubs 2: 257. 1913; in part and as to type.

The hybrid forms between A. octandra and A. sylvatica may be recognized mainly by their shrubby or small tree habit and the few stipitate glands mixed with tomentum on the pedicel and/or the lower part of the calyx. The result of introgression has been primarily an increased variation in the populations of A. sylvatica, although some reciprocal introgression takes place.

The type specimen for A. glaucescens is Harbison's no. 619, collected May 18, 1911 in Banks County, Georgia (A). This population (Harbison nos. 610, 618, 619, and 620) appears as a hybrid swarm between A. octandra and A. sylvatica, these collections and the duplicates of 619 representing different recombinants or the parent trees of A. octandra. From Sargent's description, A. glaucescens would be a synonym of A. sylvatica as defined by me, but the type specimen happens to be one of the recombinants belonging under this hybrid designation.

The hybrid forms between these two species are mostly found in the region of overlap between the parental species, in southeastern Tennessee, western North Carolina, northern Georgia, and northwestern South Carolina (Map 1).

SPECIMENS EXAMINED.—Georgia: Banks Co., Duncan & Hardin 16304 (GA); Dade Co., Duncan 2417 (GA); Dawson Co., Duncan & Adams 18538 (GA, MICH); Gordon Co., Duncan 2507 (UC); Habersham Co., Harbison 1576 (A, NCU); Hall Co., 8 May '6, Ashe (A, NY); Lumpkin Co., Duncan & Hardin 16007 (GA); Murray Co., Duncan 15770 (GA); Rabun Co., Harbison 23 (A); Stephens Co., Harbison θ (A). North Carolina: Macon Co., Harbison 211 (A); Orange Co., Apr 1896, Ashe (NCU). South Carolina: Fairfield Co., Hardin 112 (GA, MICH, NCSC); Lancaster Co., Duncan & Hardin 15610 (NCU); Oconee Co., McVaugh 5658 (A, UC). Tennessee: Franklin Co., P. H. Webb 180 (TENN); Grainger Co., 13 May 1945, S. A. Cain (TENN).

Populations of A. sylvatica are shown in Figs. 27–30; all show relatively little variation. They are found in generally undisturbed mixed hardwoods and under fairly uniform environmental conditions. The populations in Figs. 32 and 33 are A. sylvatica with a strong influence from A. octandra, and A. octandra with influence from A. sylvatica, respectively. The two populations were found in mixed hardwoods which had been cut over to some extent. The typical A. octandra, from western North Carolina, is seen in Fig. 34.

Aesculus pavia × sylvatica

Pavia mutabilis Spach, Ann. des Sci. Nat., Bot., Sér. 2, 2: 57. 1834.
Aesculus mutabilis (Spach) Schelle, in Beissner et al., Handb. Laubh.-Ben. 323, 1903.

Aesculus × harbisonii Sarg., Trees and Shrubs 2: 259. 1913.

Aesculus × mutabilis var. penduliflora Sarg., Jour. Arn. Arb. 5: 48. 1924.

Aesculus × mutabilis var. induta Sarg., l. c. 48. 1924.

Aesculus × mutabilis var. harbisonii (Sarg.) Rehd., Jour. Arn. Arb. 7: 241. 1926.

Hybrid forms between A. pavia and A. sylvatica may usually be recognized by flower color (yellow-red) and petal margins glandular-villous.

The F₁ hybrids, backcrosses and recombinants are rather common in the Piedmont and Coastal Plain of the Carolinas, Georgia and Alabama, and also northward in the Ridge and Valley Province of eastern Tennessee into southern Kentucky (Map 1). Some well known populations, e. g., around Lea Lakes in Grainger County, Tennessee, Sequatchie Valley of Tennessee (Svenson, 1941), and Stone Mountain, Georgia (Hardin, 1957), have been favorite collecting areas for many years and are now recognized as hybrid swarms. The Stone Mountain population is of particular interest since it is the type locality for a number of species and varieties.

Hybrids between A. pavia and A. sylvatica were found as early as the middle 1800's in European gardens. Many of the names listed here in synonymy were based on the hybrids which arose in cultivation, or the seeds were collected in the field and planted in the Arnold Arboretum. The various varieties of A. \times mutabilis described by Sargent represent different backcrosses or recombinants and later segregates which arose under cultivation.

SPECIMENS EXAMINED.—Alabama: Baldwin Co., J. G. Jack 2979 (US); DeKalb Co., Harbison 555 (A); Etowah Co., Harbison 543 (A, MO); Lee Co., Duncan 9174 (GA, MO). Florida: Escambia Co., Harbison 4128 (NCU); Liberty Co., yr. 1868, B. F. Saurman (PG). Georgia: Bartow Co., Duncan 8028 (GA, GH, TENN, UC, US); Bryan Co., Pryon & McVaugh 1384 (GA); Butts Co., Hardin 104 (GA, MICH, NCSC); Catoosa Co., Duncan 15764 (GA); Chatooga Co., Duncan & Hardin 15919 (GA, MICH); Cobb Co., Duncan 13489 (GA); Coweta Co., Duncan & Huttleston 10707 (GA); Crawford Co., Hardin 101 (GA, MICH, NCSC); DeKalb Co., Hardin 107 (GA, MICH, NCSC); Floyd Co., Duncan & Hardin 15252 (GA, MICH); Forsyth Co., Duncan 5268 (GA); Fulton Co., Duncan 9347 (GA); Hall Co., Duncan 18569 (GA); Hart Co., Duncan 4825 (GA, GH, MO, UC, US); Jasper Co., Apr 1842, T. C. Porter (GH); Meriwether Co., Duncan & Huttleston 10765 (GA); Muscogee Co., 14 Apr 1940, L. R. Kische (NCU); Paulding Co., Pyron & McVaugh 2599 (GA); Richmond Co., 18 Mar 1909, C. S. Sargent (A); Talbot Co., 7 Aug 1941, O. Battle (vs); Telfair Co., 9 Apr 1918, Harbison (NCU); Troup Co., Duncan & Huttleston 10793 (GA); Upson Co., A. Cronquist 4337 (GA, GH, MO, US); Whitfield Co., Duncan 15769 (GA). Kentucky: Bell Co., H. A. Gleason 8831 (NY): "southern Ky.", May-Aug 1900, Sadie F. Price 2385 (GH). North Carolina: Bladen Co., Radford 6871 (NCU); Columbus Co., C. V. Morton 2122 (US); Durham Co., Harbison 15100 (NCU); Halifax Co., Apr 1894, C. S. Williamson (PH); New Hanover Co., May 1867, W. M. Canby (MICH, PH); Orange Co., 2 May 1916, H. R. Totten (NCU); Wake Co., Harbison 7 (A). South Carolina: Anderson Co., yr. 1886, F. H. Earle

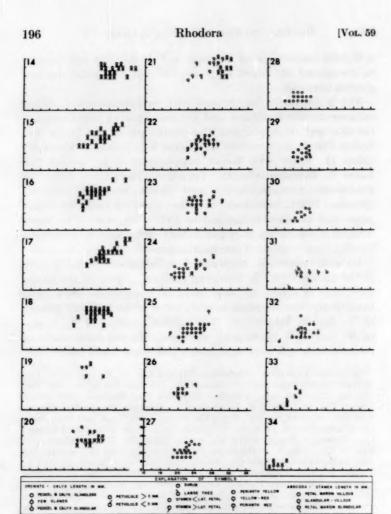


Fig. 14-34. Pictorialized scatter diagrams showing introgression between A. pavia, sylvatica and A. octandra. 14, A. pavia (Appling Co., Ga.; H. 105). 15, A. paria (Geneva Co., Ala.; H. 102). 16, A. paria (Crenshaw Co., Ala.; H. 103). 17, A. paria (Effingham Co., Ga.; H. 106). 18, A. paria (Winston Co., Ala.; H. 108). 19, A. paria (X sylvatica) (Catoosa Co., Ga.; Duncan 12350). 20, A. paria (X sylvatica) (Floyd Co., Ga.; Duncan 15750). 21, A. pavia (x sylvatica) (Crawford Co., Ga.; H. 101). 22, A. paria × sylvatica (DeKalb Co., Ga.; H. 129). 23, A. paria × sylvatica (DeKalb Co., Ga.; H. 107). 24, A. sylvatica (× paria) (Butts Co., Ga.; H. 104). 25, A. sylvatica (× pavia) (Hart Co., Ga.; H. 111). 26, A. sylvatica (× pavia) (Troup Co., Ga.; Duncan 10793). 27, A. sylvatica (Morgan Co., Ga.; Duncan 10825). 28, A. sylvatica (Union Co., S. C.; H. 113). 29, A. sylvatica (Clarke

P STREET SLAT. PETEL

(NY); Clarendon Co., W. Stone 624 (PH); Darlington Co., B. E. Smith 1615 (NCU); Dorchester Co., Duncan 5902 (GA); Oconee Co., Harbison 6 (A). Tennessee: Bledsoe Co., Shanks 1390 (TENN); Grainger Co., M. Webster 28 (GA); Marion Co., Shanks, Hardin, Woods & Barkley 15464 (TENN); Rhea Co., Sharp 19071 (TENN); Sequatchie Co., Cain & Sharp 4398 (NY, TENN); Van Buren Co., 27 Apr 1952, J. E. Byrd (TENN).

The populations of "good" A. pavia are shown in Figs. 14–18. There is some variation, in size of flowers, between populations and within single populations which is probably due to ecological conditions. Each of these populations was found in a relatively mature area under mixed hardwoods and in well-drained soils.

The populations shown in Figs. 19-21 represent A. pavia with influence from A. sylvatica. Figures 22 and 23 are the populations from Stone Mountain, Georgia, which have been previously described (Hardin, 1957). The populations in Figs. 24-26 are primarily A. sylvatica with strong influence from A. pavia. These intermediate populations for the most part were found in disturbed areas, along road sides, heavily lumbered woods, pastured lands, or the edges of cultivated farms. Aesculus sylvatica is represented in Figs. 27-30.

The reciprocal introgression between these two species has resulted in a heightened variability in the two parental species, and this gene flow has gone far into the populations of the parental species and away from the region of the original crosses (Map 1).

Aesculus octandra \times (pavia \times sylvatica)

Aesculus woerlitzensis Koehne, Repert. Sp. Nov. Reg. Veg. 11: 396. 1913.

Aesculus woerlitzensis var. ellwangeri Rehd., Mitt. Deutsch. Dendr. Ges. 1913 (22): 258. 1914.

Aesculus × dupontii Sarg., Jour. Arn. Arb. 5: 46. 1924. Aesculus × dupontii var. hessei Sarg., l. c. 47. 1924.

Occasional specimens have been seen which have characters of the three species A. octandra, A. pavia and A. sylvatica. Most of these are best represented (at least on the basis of morphological characteristics) as A. octandra × (pavia × sylvatica) and recognized by glandular-villous petal margins, yellow-red flowers, and with stipitate glands mixed with tomentum on the

Co., Ga.; H. 117). 30, A. sylvatica (Elbert Co., Ga.; H. 116). 31, A. sylvatica × octandra × pavia (Gordon Co., Ga.; Duncan 15744). 32, A. sylvatica (× octandra) (Fairfield Co., S. C.; H. 112). 33, A. octandra (× sylvatica) (Murray Co., Ga.; Duncan 15770). 34, A. octandra (Ga., N. C., Tenn.; H. 118–122, 131, 725).

pedicels and lower part of the calyx. These hybrids are not very different from the A octandra \times pavia, but the petal margins are more like the \dots avia \times sylvatica hybrid.

The specimens labeled as $A. \times dupontii$ and grown at the Arnold Arboretum and at the Botanical Gardens, University of Michigan (from the type tree in front of the DuPont mansion, Winterthur, Delaware), show characteristics of all three of these species. Just what the original crosses were, of course, is not known. Sargent, in the original description, supposed that the cross was between A. pavia and A. sylvatica, but he overlooked the important glands on the pedicels—a characteristic only of A. octandra.

Aesculus woerlitzensis, and its variety, originated in European gardens or nurseries—the actual origin is unknown. They have been cultivated in the Arnold Arboretum and other gardens in the United States for many years.

Since A. sylvatica is located in the relatively narrow Piedmont between A. octandra of the Appalachians and A. pavia of the Coastal Plain, and since the apparent gene flow from these two species extends some distance into A. sylvatica from the areas of original hybridization, occasional populations of A. sylvatica would be expected to show influence from both A. pavia and A. octandra. Such populations with various degrees of influence from the three parental species have been found (Map 1). The population in Gordon County, Georgia, is shown in Fig. 31.

SPECIMENS EXAMINED.—Georgia: Bartow Co., Duncan 8094 (GA); Forsyth Co., Duncan 5268 (GA); Gordon Co., Duncan 15744 (GA); Hall Co., Duncan 18569 (GA, MICH); Whitfield Co., Duncan 15769 (GA). North Carolina: Halifax Co., 27 Apr 1897, J. K. Small (NY). South Carolina: Lancaster Co., Duncan & Hardin 15610 (GA, NCU); Richland Co., 13 Apr 1937, J. H. Chapman (GA).

Aesculus octandra × pavia

Aesculus hybrida DC., Cat. Hort. Monsp. 75. 1813. Pavia hybrida (DC.) DC., Prod. 1: 598. 1824.

Aesculus pavia var. arguta Lindl., Bot. Reg. 993. 1826.

Pavia livida Spach, Ann. des Sci. Nat., Bot., Sér. 2, 2: 56. 1834

Pavia hybrida Spach, I. c. 57. 1834. Pavia versicolor Spach, I. c. 57. 1834.

Pavia lindleyana Spach, l. c. 57. 1834. Pavia lindleyana Spach, l. c. 59. 1834.

Pavia arguta (Lindl.) Raf., Alsog. Am. 74. 1838.

Aesculus versicolor Wenderoth, Ind. Sem. Hort. Acad. Marburg. 1853: 4. 1853.

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Aesculus flava var. purpurascens Gray, Man. Bot. N. U. S., ed. 2, 83.
1856.

Aesculus octandra var. hybrida Sarg., Silva No. Amer. 2: 60. 1891.

Aesculus octandra var. purpurascens (Gray) Schneider, Ill. Handb.

Laubh. 2: 252. 1912.

This hybrid is recognized by flower color (red-yellow), the stipitate glands on the pedicel and glandular-pubescent petal margin.

No natural hybrids between these two species have been recognized. Garden hybrids, however, representing this cross have long been in cultivation. Sargent (1913) states that A. hybrida appeared in the Botanic Garden at Montpelier early in the nineteenth century. It is now cultivated in many varieties in Europe and to a lesser extent in America.

Early records of A. hybrida (or synonym) from West Virginia, Virginia and Maryland are probably based on the cultivated hybrids of European origin. Sargent (1913) presents a clear account of the history of these hybrids and the confusion which they have brought about in the nomenclature of the natural populations in eastern America.

With sympatric introgression occurring in these species of section Pavia, the identity of the entities is maintained by ecological and/or internal barriers of various kinds. The effectiveness or strength of these barriers (whatever they may be) varies among the different crosses. For example, introgression between A. glabra and A. pavia is apparently quite restricted, while, on the other hand, the introgression between A. glabra and A. octandra is widespread. Where the barriers to crossing are slight, an increased variability in the participating populations is brought about by the segregation and independent assortment of the various genes and alleles. Although the influence is mainly on one of the parents, reciprocal introgression does occur in all cases in varying degrees.

The significant point is that even with such a great amount of gene flow into certain species (e. g., A. sylvatica), they remain distinct. Heiser (1949), in discussing such species, states that "perhaps the ability to remain distinct in spite of hybridization entitles them rightfully to the designation of 'species'." The apparent discontinuity in breeding, which keeps these entities

apart, is, in my opinion, a very important criterion for the recognition of the species in Aesculus section Pavia.

It is thought that introgression in section Pavia has been going on during relatively recent times only. Presumably these species arose by allopatric speciation possibly in the Appalachians, and evolved independently for some time, but without developing complete barriers to interbreeding. During or after Pleistocene the species ranges came together—because of expanding ranges and/or migrations of the populations. Once sympatric, introgression could proceed.

Introgression may be of primary importance as a factor in the future evolution of the eastern buckeyes. With continued gene flow and heightened variability within the populations, there is an increased plasticity of the species—a plasticity which may make for increased survival value in the face of changing environmental conditions.

In connection with the analysis of hybridization in Aesculus, the cytology, or more specifically the karyology, of the genus was studied. Although cytological studies are rather monotonous in this genus, the study of chromosomes—number and morphology plus their meiotic behavior—does, to some extent, aid in indicating hybridization between species.

Very little cytological investigation was undertaken during the course of this study, but the chromosome number (n = 20) was checked in many specimens representing six of the species. It was hoped that chromosome counts of A. parryi, A. californica and Billia spp. could be made, but this was not accomplished because of the lack of adequate living material. No published counts have been found for the above or for A. indica, A. assamica or A. turbinata. A tentative count was made from root tips and anthers of A. californica, but in each case the count of 2n = 40 and n = 20 was somewhat subjective. The numbers in all other species as well as in many of the described hybrids and, now unrecognized, varieties and species, have been reported by one or more authors (Darlington and Wylie, 1956; Gaiser, 1930, 1930a; Seitz, 1951; Wang, 1939).

The only reported differences in the chromosome number in the family are for A. carnea and A. plantierensis, which have been mentioned earlier. According to Upcott (1936), secondary pairing and the occasional formation of quadrivalents, suggests that possibly the parents are tetraploids and therefore A. carnea is actually an octoploid and A. plantierensis a hexaploid. Stebbins (1950) refers to this by using Aesculus as one of the examples of a genus in temperate regions of which the base number (x = 20) is probably of ancient polyploid derivation.

Individual chromosomes of a karyotype in Aesculus do not vary markedly in shape or size (Hoar, 1927); there are, however, slight differences in the chromosome size of different species. Skovsted (1929) found a recognizable difference in size between A. hippocastanum, A. glabra and A. parviflora, all of which have relatively small chromosomes, and A. pavia and A. octandra,

which have larger ones.

Probably the most significant evidence to come from cytological investigations of Aesculus has been the recognition of meiotic irregularities. These are discussed particularly by Hoar (1927) and to some extent by Pelletier (1935). Hoar recognized no irregularities in the "good" species, but in others, lagging chromosomes and polyspory were common, and the percentages of abortive pollen were high. He found that such irregularities in meiosis and pollen formation were common in both artificial and natural hybrids. He therefore concluded that such irregularities found in Aesculus specimens placed "their ancestry under suspicion." I have checked the frequencies of abortive pollen in numerous specimens. Those recognized by floral characters as being of hybrid origin have high percentages of abortive pollen, and those identified as "good species" have all viable pollen or only a very low percentage of abortives. This agrees entirely with the present concepts of the species, and is additional evidence for introgression between species in the section Pavia.

Hoar (1927) raised one interesting question concerning the propagation of the plants with high precentages of abortive pollen. Some are clonal, propagated to some extent by root sprouts, but there is no indication of apomictic seed production in any of the species. Obviously, there is enough viable pollen to result in a number of seeds each season. A perennial plant such as the buckeye is not dependent on a great quantity of seeds each season for survival. The great number of abortive pollen grains, however, could result in an incomplete fertilization.

which has been suggested earlier (Hardin, 1955) as a possible cause for the relatively few seeds which are produced per capsule.

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A REVISION OF THE VERNAL SPECIES OF HELENIUM (COMPOSITAE)

HOWARD F. L. ROCK

(continued from p. 178)

To complete the confusion, since 1874 both Galardia fimbriata Michx. and Leptopoda fimbriata T. & G. have often been considered to be the same taxon, despite the inadequate understanding of either the nomenclatural or taxonomic complexities surrounding both of the binomials. This has led to a confused application of both Wood's H. fimbriatum and Gray's H. fimbriatum to various taxa to be found from the Carolinas to Texas. Moreover, the parenthetical author has been variously cited as either Michaux or Torrey and Gray or else left out completely. Nevertheless, the taxon described by Torrey and Gray as Leptopoda fimbriata is recognized here as a distinct species and that this species is not the same as either of the two elements (H. vernale and H. pinnatifidum) included within Galardia fimbriata Michx.

There appears, then, to be only one course of action possible under the provisions of the rules and preamble of the present Code. This course of action is to invoke the application of Article 65 by which an ambiguous name must be rejected. Therefore the name *Helenium fimbriatum* is hereby rejected from use for this species. In order to avoid futher confusion and inasmuch as Thomas Drummond was the first person to collect this plant, the epithet *Drummondii* has been chosen to form the new name *Helenium Drummondii* for this species.

Helenium Drummondii is most likely to be confused, upon superficial examination, with Helenium vernale. The character of the pappus, however, is sufficient to result in a ready separation of the two. In H. Drummondii it is usually longer and always distinctively slashed into a multitude of fimbriae, the fimbriae

forming over one-half the body of the scale and being crimped or crinkled. The hairy-pubescent achenes, the longer and narrower ray corollas and the lanulose pubescence at the top of the peduncle in *H. Drummondii* reinforce the distinction between the two. *Helenium Drummondii* may be distinguished from *H. pinnatifidum* on the basis of the more-decurrent cauline leaves, the petioloid radical leaves, the longer and narrower ray corollas and the characters of the pappus scales.

The two specimens of this species reputedly from Florida pose a distributional problem in that all the other specimens of this species are either from Texas or western Louisiana. There is no definite locality given for these two specimens other than "Florida" or "East Florida." In addition, as far as this study has revealed, this species has not been collected in Florida apart from these two specimens nor since 1876. As near as can be determined, the two specimens belong to the taxon H. Drummondii and there is no reason for considering them as otherwise. They may possibly represent a "lost" element of the Floridian flora that is now either extinct or very highly restricted in distribution so as not to have been re-collected.

However, at the Gray Herbarium there is a specimen of this species which was collected by Leavenworth in Texas "near the Salina [or Sabine]." This specimen is the syntype of Leptopoda fimbriata T. & G. that was acknowledged by Torrey and Gray to be from Texas. It seems highly probable that the syntype collection by Leavenworth from East Florida represents a mislabeling as to locality of collection, and may well be a duplicate collection of the one made in Texas.

The specimen collected by Mary Treat is not so easily explained or dismissed for there is no indication that she ever was in Texas or Louisiana collecting plants. In this particular case, it may well be that the Treat collection is the result of a chance introduction of *H. Drummondii* to the eastern coast of Florida and Mrs. Treat happened to be there one late winter to collect it. A more extreme possibility is that these two specimens represent a second origination of *Helenium Drummondii* from either *H. vernale* or *H. pinnatifidum* in the eastern part of Florida and are not directly related to *H. Drummondii* of Texas and Louisiana.

4. Helenium brevifolium (Nutt.) A. Wood

Leptopoda brevifolia Nutt. Trans. Am. Phil. Soc. ser. 2. 7: 373. 1841. Syntype: collected by DeSchweinitz, Yadkin (рн). Syntype (вм—not seen).

Leptopoda brevifolia Nutt. var. β T. & G. Fl. N. A. 2: 387. 1842. Lectotype: "Leptopoda? integrifolia, L. brevifolia Nutt., Raleigh, N. C.,

M. A. Curtis" (NY).

Helenium brevifolium (Nutt.) A. Wood, Am. Bot. & Fl. 182. 1870.
Helenium brevifolium (Nutt.) A. Gray, Proc. Am. Acad. Arts & Sci.
9: 205. 1874. Superfluous name repeating the combination of A. Wood.
Helenium Curtisii A. Gray, Proc. Am. Acad. Arts & Sci. 9: 204. 1874.
Lectotype: "Leptopoda brevifolia, Raleigh, N. C., M. A. Curtis" (GH).

Heleniastrum brevifolium (A. Gray) O. Ktze. Rev. Gen. (pt. 1) 342. 1891. Heleniastrum Curtisii (A. Gray) O. Ktze. Rev. Gen. (pt. 1) 342. 1891. Helenium integrifolium Mohr, Contrib. Nat. Herb. 6: 811. (1901) non

Sesse & Moc. Fl. Mex. 189. 1894.

Perennial herb, the stem developing from a rosette formed the previous season from the seedling or as an offset from the short caudex; caudex with coarsely fibrous roots and often with the persistent fibrous leaf bases of prior rosettes. Plant erect, (2.2-) 3.2-7.2 (-10.0) dm. high, single-stemmed, often occurring in clusters, branched, each branch bearing but a single head. While the growth is of a determinate type, with a head terminating each branch and the successive branches developing from the upper leaf axils, the over-all pattern of the branching system is of the type commonly referred to as "corymbosely branched." Heads 1-4 in number, the larger number occurring on the more robust plants. Stems sulcate, glabrous and often anthocyanaceous below, becoming increasingly striate above. Peduncle striate, lanulose below, becoming increasingly pubescent upwards so as to be lanose to tomentose at the base of the involucre in extreme cases. Lateral peduncles increasing in length with a decreased position on the stem, often over-topping the terminal or central peduncle. Peduncles not noticeably enlarged or fistulous beneath the involucre. Leaves, except for the uppermost ones, glabrous, uni-nerved with the lateral nerves obscured, impressed-punctate, resin-atomiferous, gradually reduced upwards in the more robust plants, but often appearing scapose in the more depauperate plants. Radical leaves obovate, spathulate to oblanceolate, usually intact and present; margin entire, repand, scalloped, scalloped-denticulate to shallowly incised; apex obtuse to more or less acute; the basal portion tapering to form a petioloid structure, enlarging again within the rosette so as to be somewhat clasping; (2.5-) 4.0-10.5 (-18.0) cm. long, (0.8-) 1.2-2.0 (-2.5) cm. wide. Cauline leaves becoming reduced in size and more spathulate to linear-lanceolate; margin somewhat denticulate: bases decurrent along the stem so as to form a manifest wing. The uppermost bracts are often lanulose, especially toward the base where the axil is often arachnoid-pubescent along with the adjacent stem portions. Developing buds usually quite tomentose but becoming

decreasingly so with age and development. Involucre biseriate, the outer series exceeding the inner; phyllaries linear-lanceolate, 4.0-6.0 mm. long, 1.0-2.0 mm. wide at the base, pubescent, acuminate, becoming withered and reflexed or not reflexed with age. Heads convex to mostly hemispherical, 1.2-2.0 cm. wide, 1.0-1.5 cm. high; receptacle convex to subglobose. Ray florets neutral; ligules yellow, 1.5-1.9 cm. long, pubescent below, broadly cuneate, 3-4-fid at the apex, resin-atomiferous; achenes abortive and less than those of the disk in size. Disk brown, decidedly so to sometimes only faintly, especially in dried specimens when it then appears to be a sordid-yellow. Disk florets fertile; corollas pentamerous, 3.0-5.0 mm. long, the lobes pubescent-glandular and red-purple to red brown in color, resin-atomiferous, and with a short basal tube; pappus scales obovate, somewhat clawed as a rule, verging to oblanceolate, obtuse, (1.0-) 1.5 (-2.0) mm. long, the margin more or less entire, 5-10 in number: achenes hairy-pubescent on the ribs, resin-atomiferous, 1.0-1.5 mm. long, columnar to truncate-turbinate in shape.

DISTRIBUTION: Plants of scattered localities in the Southeastern United States; occurring in upland bogs, swamps and wet depressions in the inner Piedmont-lower Appalachian provinces of North Carolina, Georgia and Alabama, Coastal Plain-like habitats of the Piedmont of North Carolina and Alabama such as Sarracenia-type bogs, wet pine woods and wet meadows, as well as in the Coastal Plain proper of southeastern Virginia, southeastern North Carolina, the western part of the panhandle of Florida, and Alabama, Mississippi and Louisiana in such habitats as wet pine barrens, Sarracenia bogs, shrub-bogs, margins of ponds, swamps

and wet ditches. (Map 2)

REPRESENTATIVE SPECIMENS.—Louisiana. St. Tammany Parish: Slidell, 2 April 1887, Joor s.n. (NO), Mississippi. Harrison Co.: near Biloxi, Perkins & Hall 2845 (POM). Jackson Co.: Ocean Springs, April 1892, Skehan s.n. (DUKE, GH, IA, MO, NCU, SMU, WIS). Alabama. Baldwin Co.: Point Clear, Rte. 98, S. of Fairhope, Hood 4518 (FLAS). Cherokee Co.: about 2 m. NE. of Center, Harper 91 (GH, MO, NY). Cullman Co.: about 4 m. ENE. of Cullman, Harper 3724 (GH, MICH, MO, PH, US). Escambia Co.: Flomaton, Bilt. Herb. distrib. 9588a (GH, MIN, NCU, POM). Lee Co.: Auburn, 9 May 1896, Earle & Underwood s.n. (NY). Mobile Co.: Mobile, 26 April 1898, Baker s.n. (F, NY, POM). Russell Co.: near Fort Mitchell, Harper 2 (GH, MO, NY, PH). Washington Co.: 3.8 m. NW. of Citronelle, Cory 58563 (NCSC, SMU). Florida. Escambia Co.: Ensley, Goodale 69874 (GH). Okaloosa Co.: 6 m. NW. of Fort Walton, Tyson 583 (FLAS). Santa Rosa Co.: Milton, Fassett 21170 (MIN, WIS). Walton Co.: DeFuniack Springs, Curtiss 6383 (BKL, F, GH, MIN, NY, UC, US). Washington Co.: 10 m. N. of Ebro, Rte, 79. Hood 1678 (FLAS). Georgia. Douglas Co.: 1.3 m. W. of Villa Rica, McDowell & Venard 579 (DUKE). Meriwether Co.: Peters, Twomey s.n. (PH). North Carolina. Brunswick Co.: near Maco, along Rte. 74-76, Godfrey & Weibe 50368 (DUKE, GH, NCSC, SMU, WS). Catawba Co.: N. of Hickory, Small & Heller 447 (F, MO, NY, PENN, PH, UC, US). Henderson Co.: East Flat Rock, Correll, Blomquist & Garren 5145 (DUKE). Iredell Co.: 3.2 m. W. of Harmony, Radford 2655 (NCU). New Hanover Co.: Wilmington, M. A. Curtis s.n. (PH). Wake Co.: sphagnous bog at Method, Raleigh, Godfrey 3974 (NCSC, NCU, NY).

Virginia. Greensville Co.: N. of Dahlia, Fernald & Long 10051 (F, GH, MO, NY, US). James City Co.: about 3 m. W. of Williamsburg, Baldwin, Jr. 14861 (DUKE, MO, NCSC, NY, US).

In the North American Flora Torrey and Gray established a variety within this taxon, variety β , a reputedly very local endemic from the vicinity of Raleigh, North Carolina. The variety differed from the more typical part of the species in that it was more robust, i.e. "stem stouter and taller; leaves larger; the cauline more strongly decurrent." Asa Gray, 32 years later, elevated the variety to specific status using the name Helenium Curtisii and added as diagnostic characters for the separation of the two, the distinction that H. Curtisii had an ovate-conical receptacle and that the disk was subglobose. This was in contra-distinction to the barely hemispherical receptacle and convex disk of H. brevifolium.

The present study could not validate the characters adduced by Torrey and/or Gray for the separation of these two taxa, Helenium brevifolium and Helenium Curtisii, except to the extent that in the same population some of the plants are more robust than some of the others. Consequently, no formal taxonomic recognition is given in this treatment to Helenium

Curtisii as a taxon apart from Helenium brevifolium.

Unfortunately it is no longer possible to collect "Curtisii" at the type locality. In the late spring of 1955 the author made a trip to the vicinity in an effort to relocate it. The type locality was known by hearsay to be a bog just outside of Raleigh. close by Meridith College in a suburban area known as Method. Several boggy spots were located, including a known Coastal Plain-like one containing Sarracenia flava but not "H. Curtisii." On a second trip, the correct location, as far as it could be determined, was finally located and the reason for the difficulty in finding it was apparent. Where once had been a sphagnous bog with Coastal Plain-like aspects was now a paved street with two rows of half-completed houses on each side. The type locality, with whatever "Curtisii" that might have persisted through the years, had been bull-dozed from existence. All that remained of the bog were some springy places in the new back-yards of the houses.

Several other locations are now known in North Carolina,

however, and in Virginia where Helenium brevifolium occurs. Specimens collected from these populations have been identified and accepted as "Curtisii" in the past. Indeed, it takes no imagination or struggling with the keys to identify many of the specimens of H. brevifolium from the Coastal Plain of Florida, Alabama, Mississippi and North Carolina as "Curtisii" while duplicates of the same collections pass as H. brevifolium. The author has visited three of these locations in Iredell Co., N. C. and has had the advantage of observing the "Curtisii" element in the field and making mass collections. If, in the field, one were to collect along a line-transect through one of the boggy areas that is somewhat open and subject to seasonal dryingout in the late spring and early summer, the relationship of these two elements, H. brevifolium and "Curtisii" is clearly Those plants from the outer, drier edges of the bog would be identified as H. brevifolium. The plants from the center of the bog, where the water is more plentiful and present for the longest period of time, however, would be identified as "Curtisii." Those plants from the far side of the bog, where a drier area is again encountered, would in turn be identified, once more, as H. brevifolium. Those plants from between the center and the outer edges, as well as those from tussock portions of the bog, grade off from the aspect of brevifolium to that of "Curtisii." In those bogs where the water is plentiful all season. more of the plants would be identified as "Curtisii" than not, especially from those bogs that are deep in ravines and shaded by overhead hardwoods. It would appear, then, that the "Curtisii" element is no more than a growth form of H. brevifolium induced by highly mesophytic conditions.

Helenium brevifolium is easily distinguished from H. pinnatifidum, H. vernale and H. Drummondii on the basis of the following characters:

- the red-brown tipped disk florets so that the disk is red-brown colored
- the corymbose branching habit, with the branches terminated by a single head
- the obovate and more or less clawed pappus scales.

Helenium brevifolium can, in turn, be distinguished from the other taxon with which it might be confused, H. campestre, on the basis of:

1. the achene is hairy-pubescent rather than puberulent

- the pappus scales are twice as long, 1 mm. long or more in contrast to 0.5 mm
- 3. the stem and foliage, excepting the uppermost, are glabrous

4. the radical leaves are petioloid.

5. Helenium campestre Small

Helenium campestre Small, Fl. SE. U. S., 1291. 1903. Holotype: Collected by Dr. Hasse, 25 May 1885, Little Rock, Pulaski Co., Arkansas (NY).

Perennial herb, the stem developing from a basal rosette formed the previous season from the seedling or as an offset from the short caudex; caudex with coarsely fibrous roots and often with the persistent fibrous leaf bases of prior rosettes. Plant erect, 4.0-6.7 dm. high, single-stemmed. branched, each branch usually bearing but a single head, though in the more robust plants the branches are sometimes bifid toward the apex and thus bearing two heads. While the growth is of a determinate type, with a head terminating each branch and the successive branches arising from the upper leaf axils, the over-all pattern of the inflorescence is of the type commonly termed corymbosely branched. Heads 1-8 in number, the more robust plants with the greater number, and usually quite showy by virtue of the large rays. Stems sulcate, winged and noticeably hirsute below, becoming striate and finely pubescent above. Peduncles striate, becoming densely pubescent above, lateral ones becoming longer with descending position on the stem, usually equal to the central one, and becoming enlarged and fistulous beneath the involucre. Leaves decidedly hairy-pubescent, uninerved with the lateral nerves obscured, impressedpunctate, resin-atomiferous, becoming gradually reduced upwards. Radical leaves obovate, spathulate, oblanceolate, to elliptic-lanceolate, usually intact and present; margin entire to repand, occasionally scalloped or pinnatifid-incised; apex obtuse; the basal portion not petioloid but gradually tapered and becoming enlarged again within the rosette so as to be somewhat clasping; 3.5-7.0 cm. long, 0.5-1.7 cm. wide. Cauline leaves becoming reduced upwards; not petioloid; bases decurrent along the stem so as to manifest a wing; oblanceolate, elliptic-lanceolate to linear-lanceolate; margin entire to repand, the uppermost bracteate ones occasionally somewhat denticulate; apex acute to slightly acuminate; base gradually tapered to the wing; usually less coarsely pubescent than the basal leaves. Involucre biseriate, the outer series exceeding the inner; less deeply parted than in preceding taxa so as to form a slight cupule at the base; phyllaries linear-lanceolate, 5.0-6.5 mm. long, 1.5-2.0 (-3.5) mm. wide at the base, pubescent, acute to acuminate, becoming more or less reflexed ultimately. Heads mostly hemispherical to subglobose, 0.8-1.5 cm. high, 1.0-2.0 cm. wide; receptacle mostly subglobose though often hemispherical. Ray florets neutral; ligules yellow, prominent and showy, resin-atomiferous and pubescent below, 1.5-2.5 cm. long; achenes abortive and less than those of the disk in length. Disk brown; disk

florets fertile; corollas 3.0–4.5 mm. long, brown-tipped on the lobes, glandular-pubescent on the lobes, pentamerous, resin-atomiferous, cylindric to cylindric-campanulate in outline with a short basal tube; pappus oborate to suborbicular, not clawed, 5–10 in number, 0.4–0.5 mm. long, obtuse at the apex, margin entire to erose; achenes puberulent on the ribs, resin-atomiferous, 1.0–1.5 mm. long, columnar to truncate-turbinate in shape.

DISTRIBUTION: Known only from seven counties of eastern Arkansas, between the Ouachita Mountains and the Mississippi Alluvial Plain; occurring in low open pinewoods, fertile bottoms, flatwoods, wet pinelands, rocky open woods, river bottoms, ridge thickets and moist places

in prairies. (MAP 2)

REPRESENTATIVE SPECIMENS.—Arkansas. Drew Co.: Wilmar, Demaree 15057 (F, GH, MIN, MO, NY). Faulkner Co.: near Conway, Palmer 27110 (MO, UARK). Independence Co.: Batesville, Demaree 26766 (OKLA, SMU, TEX). Prairie Co.: Grand Prairie near Hazen, Palmer 25064 (GH, NY). Pulaski Co.: base of Maumelle Mountain near Pinnacle, Palmer 22993 (F, MO, UARK). St. Francis Co.: Forrest City, Demaree 15116 (F). White Co.: W. Bradford, Moore 450469 (UARK).

Until this species was recognized as being distinct by J. K. Small, it had been confused most often with Helenium flexuosum Raf. (H. nudiflorum Nutt.). It can be distinguished at a glance by the corymbose branching habit and the small number of large heads in contrast to the paniculate branching and large number of small heads of H. flexuosum. The characters by which H. campestre may be distinguished from H. brevifolium have been pointed out under the treatment of the latter. While H. campestre has been most often confused with H. flexuosum, its closest affinity appears to be with H. brevifolium. Much of the discussion related to this taxon has already been brought out in relation with that of H. brevifolium and H. campestre in the portion of this paper devoted to relationships.

6. Helenium flexuosum Raf.

Helenium flexuosum Raf. New Fl. N. A. (pt. 4): 81. 1838. Neotype: Collected by Mary and Emily Mohr, Aug. 1884, Terre Haute, Vigo County, Indiana (us); original type locality ascribed by Rafinesque was the "River Wabash."

Helenium dichotomum Raf. New Fl. N. A. (pt. 4): 81. 1838.

Helenium nudiflorum Nutt. Trans. Am. Phil. Soc. ser. 2. 7: 384. 1841. Syntype: "Helenium*nudiflorum (Nutt.) Ark." (рн); Syntype: "Helenium*nudiflorum, Red River" collected by Nuttall, ex herb. Elias Durand (gн); Syntype: (вм—not seen).

Helenium micranthum Nutt. Trans. Am. Phil. Soc. ser. 2. 7: 385.

1841. No type material located.

Leptopoda brachypoda T. & G. Fl. N. A. 2: 388. 1842. Lectotype: Collected in Louisiana, Aug. 1840, by Dr. Hale (NY).

Leptopoda brachypoda T. & G. var. β. T. & G. Fl. N. A. 2: 388. 1842.

Lectotype: Collected in Louisiana by Dr. Leavenworth (NY).

Helenium atropurpureum Kth. & Bouché, Ind. Sem. Hort. Berol. Anno 1845 Collectorum 12. 1845. Type: original description; cultivar. Helenium atropurpureum Kth. & Bouché var. grandicephalum LeMaire, L'Ill. Hort. 10: 375. 1863. Type: illustration and original description; cultivar.

Helenium seminariense Featherman, Rep. So. & Cent. La. 1870, Fl.

Ludov. 74. 1871. Lectotype: "Helenium seminariense" (GH).

Helenium brachypoda (T. & G.) A. Wood, Am. Bot. & Fl. 182. 1870.
Helenium nudiflorum Nutt. var. purpurea Hale ex. A. Gray, Proc. Am. Acad. Arts & Sci. 9: 203. 1874. Type: the same as L. brachypoda T. & G. var. β. T. & G.

Heleniastrum nudiflorum (Nutt.) O. Ktze. Rev. Gen. (pt. 1) 342. 1891. Helenium polyphyllum Small, Fl. SE. U. S. 1291. 1903. Holotype: Collected by S. M. Bain, no. 77, Sept. 1892. Jackson, Madison County, Tenn. (NY); isotype (?), (US).

Helenium Godfreyi Fern. Rhodora 45: 494. 1943. Holotype: Collected by Godfrey & Tryon, no. 586, 14 July 1939, Pineville, Berkeley

County, S. C. (GH); isotypes (NY, UC, US).

Helenium floridanum Fern. Rhodora 45: 494. 1943. Holotype: Collected by A. H. Curtiss, no. 6663, Fitzgerald, Hernando County, Fla. (gh); isotypes (bkl., min, mo, ny, uc, us); var. aphanactis on the label of

Curtiss 6663 is an unpublished name.

Perennial herb, stem developing from a rosette formed the previous season from the seedling or as an offset from the short caudex; caudex with coarsely fibrous roots and often with the persistent fibrous leaf bases of prior rosettes. Plant erect, 0.3-1.0 m. high, single-stemmed, usually profusely branched, each branch bearing several small heads and quite often bifid toward the apex. While the growth is of a determinate type, with each branch terminated by a head, the successive branches develop basipetally from the upper leaf axils, and while the heads are formed in a like manner on each branch, the over-all pattern of the inflorescence is of the type commonly termed paniculately-branched. Heads usually very many, with the depauperate plants having fewer in number, rarely reduced to one. Stems sulcate, pubescent, winged below, becoming striate and more broadly winged above and within the branching portion, with the wings sometimes over 5 mm. wide and the pubescence usually becoming more fine and incurved. Peduncles striate, with short incurved pubescence, more or less uniform in length and becoming enlarged at the base of the involucre and fistulous, especially at maturity. Leaves with various degrees of pubescence below, ranging from glabrate to rather densely hairy, the upper leaves usually pubescent with short and somewhat incurved hairs. Leaves prominently uninerved, lateral nerves obscure, impressed-punctate, resin-atomiferous, gradually reduced upwards. Radical leaves linear-lanceolate, elliptic-lanceolate, oblanceolate to

spathulate, usually intact and present on those plants collected early in the season only; margin ranging from entire to pinnatifid-incised; apex obtuse to acute, the basal portion tapering somewhat but not petioloid, re-expanding within the rosette so as to be somewhat clasping; 3.0-21.0 cm. long, 0.4-3.0 cm. wide. Cauline leaves becoming reduced upwards. becoming more linear-lanceolate upwards, not petioloid, but decurrent along the stem so as to form a manifest wing; lower ones denticulate, but soon becoming entire; the upper bracteate leaves lanceolate to linearlanceolate, entire decurrent, more remote and often with extremely reduced bracts scattered along the peduncle. Involucre biseriate, the outer series exceeding the inner one and not so deeply parted, forming a slight cupule at the base; phyllaries linear-lanceolate, pubescent, acute to acuminate, becoming reflexed including the cupule-like portion of the base at anthesis, 0.4-0.7 cm. long, 1.0-2.0 mm. wide at the base. Heads subglobose to globose; occasionally somewhat conic; receptacle subglobose to decidedly conical. Ray florets neutral; ligules yellow, umber, suffused with red or deep purple or ligules absent entirely in some plants, resinatomiferous, pubescent below, 1.0-2.1 cm. long; achenes abortive and less than those of the disk in length. Disk red-brown to red-purple in color, 0.7-2.0 cm, wide, 0.5-1.5 cm, high; disk florets fertile; corolla 2-3.0 mm. long, glandular-pubescent on the lobes, predominently 4-merous (both lobes and stamens), red-brown to red-purple tipped, cylindric to cylindric-campanulate in shape with a short basal tube, resin-atomiferous; pappus scales 5 (-8) in number, rigid, lanceolate, usually acute at the apex so as to form an awn, the costa more or less manifest, margins serrate to a degree, 0.4-1.5 mm. long; achenes hairy-pubescent on the ribs, resinatomiferous, 1.0-1.5 mm. long, columnar to truncate-turbinate in shape. DISTRIBUTION: Plants of various provinces of the eastern United States, from just east of the Great Plains to the eastern seaboard; a weedy plant apparently extending its range northward and eastward and seemingly capable of survival in a variety of habitats; occurring in prairies, flatwoods, pine barrens, borders of ponds and stream banks, low moist woods, open areas of the Appalachians, savannahs, pocosin margins, roadsides, old fields and moist low meadows and roadside ditches; from eastern Texas northward into Missouri and Illinois and thence eastward to the

REPRESENTATIVE SPECIMENS.—Texas. Bowie Co.: 3 m. W. of Noah, Cory 56009 (NDA, OKLA, SMU, US, WS). Jasper Co.: 8 m. S. of Kirbyville, Shinners 7675 (ARIZ, GH, SMU, UC). Arkansas. Garland Co.: Hot Springs, 5 Aug. 1879, Letterman s.n. (BKL, F, MIN, MO, NY, PH, TEX, UARK, US). Leflore Co.: near Page, Blakely 1438 (DS, GH, MIN, MO, OKLA, US). Oklahoma. Adair Co.: 6 m. S. of Ballard, Waterfall 10194 (ARIZ, OKLA, RSA, SMU, TAES). Missouri. Ripley Co.: Pleasant Grove, MacKenzie 242 (COLO, F, MIN, MO, NY, PH, RM, US). Tennessee. Obion Co.: near Walnut Log, Reelfoot Lake, Eyles & Eyles 131 (FLAS, GH, MO, NY, OKLA, OKLA, OSC, PENN, TENN, REX, UC, WIS, WS, WVA). Kentucky. Lyon Co.: Kuttawa, Eggleston 5179 (GH, MIN, MO, NY). Illinois. Clinton Co.: Carlyle, Buckley s.n. (GH, NY). Indiana. Morgan Co.: Sycamore Creek, Friesner 14816 (DUKE, GA, GH, NY, UC, WS, WVAS).

Atlantic seaboard, Florida to Maine. (MAP 3)

Switzerland Co.: 1.2 m. E. of Fairview, Friesner 23581 (FLAS, NCSC, SMU, TEX). West Virginia. Upshur Co.: Sago, 15 Aug. 1947, Grose & Grose s.n. (FLAS, GA, GH, IA, NCSC, OKLA, OSC, PENN, SMU, TEX, UC, WS, WVA). Louisiana. Rapides Parish: vicinity of Alexander, Ball 506 (F, GH, MIN, MO, NY, US). Mississippi. No county indicated or determinable: Westfield, Tracy 8669 (F, GH, MIN, MO, NY, PENN, TAES, US, WIS). Florida. Duval Co.: Jacksonville, Lighthipe 559 (BKL, GH, MIN, NDA, NY, RM, WIS). Hillsborough Co.: Tampa, Curtiss 1520 (BKL, F, IA, MIN, NCSC, NY, PH, US). Georgia. Rabun Co.: Tally Mtn. Creek, Duncan 10139 (Flas, Ga, Gh, IA, MIN, MO, NCSC, NDA, SMU, TEX, UC). South Carolina. Georgetown Co.: 4 m. W. of Georgetown, Godfrey & Tryon 124 (DUKE, F, GH, NY, PENN, TENN, UC, US). North Carolina. Hertford Co.: 2 m. N. of Murfreesboro, Godfrey & Fox 49667 (DUKE, GH, MIN, WS). Macon Co.: Horse Cove, near Highlands, Godfrey 51366 (MIN, NY, OKL, OKLA, PENN, SMU, TEX, UC). Virginia. Greensville Co.: NE. of Emporia. Fernald & Long 10451 (GH, NY). Pennsylvania. Chester Co.: 11/4 m. S. of Ercildoun, Fogg 5760 (GH, PENN, TENN). New Jersey. Burlington Co.: 1½ m. E. of Red Lion, Fogg 9137 (PENN). New York. Westchester Co.: Tibbet Brook Park, Yonkers, Monachino 104 (BKL, DUKE, TENN, NY). Connecticut. Middlesex Co.: Killingworth, Weatherby 5438 (NEBC). Massachusetts. Berkshire Co.: Great Barrington, 20 July 1920, Hoffman s.n. (NEBC). Plymouth Co.: Duxbury, 6 Oct. 1902, Bond s.n. (NEBC). Vermont. Windsor Co.: Woodstock, 27 Aug. 1938, Kittredge s.n. (GH, NEBC). New Hampshire. Carroll Co.: Wonalancet, Aug. 1914, Terry s.n. (NEBC). Maine. York Co.: N. Berwick, Aug. 1896 Parlin s.n. (MIN, NEBC).

In the Synoptical Flora of 1884, Asa Gray justly considered the applicable binomials extant at that time to be mere variants and treated Helenium flexuosum as a single, polymorphous species. Subsequent to Gray, three taxa have been segregated from Helenium flexuosum and described as new species. The first of these, H. polyphyllum Small, was given specific status purely on the basis that the upper branches were more widely winged (2 mm. wide or more) and that the plant was finely pubescent as opposed to puberulent and wings of the upper branches less than 2 mm. wide. Rydberg maintained Small's H. polyphyllum as a species co-existent with H. flexuosum in the more western and southwestern part of the latter's range, rather than as the Tennessee-Georgia endemic of Small. Fernald has rightly stated (RHODORA 45: 493. 1943) that both can be maintained as separate species: "Only by recognizing the smallest specimens with narrowest cauline wings as the former [H. flexuosum], the largest ones with the broadest wings as the latter [H. polyphyllum], ignoring the large series of transitional specimens . . ." Indeed, from the author's own experience of growing members of this taxon in the greenhouse. both forms of the wing occur in plants collected in the same

locality, plants that grew so close together in the wild that they probably originated from achenes shed from the same head. The author is convinced that very little value can be attached to "finely pubescent" in contrast to "puberulent" as a taxonomic character at the specific level in this variable species. On the basis then of the widespread series of intergrades as well as because these intergrades occur within the same colony of plants no taxonomic recognition is here afforded to H. poly-phyllum.

Professor Fernald, after taking Rydberg to task for maintaining H. polyphyllum as distinct from H. flexuosum, proceeded to give specific status to two other forms of H. flexuosum that he considered worthy of such recognition (Rhodora 45: 494. 1943.) Fernald recognized these two, H. Godfreyi and H. floridanum, stating: "in our Southeast there are two extremes, native of low woods and swamps and evidently local endemics,

which seem to be really well defined species."

Helenium Godfreyi was characterized as having blunt and awnless pappus scales, which also were either round or oval and from 0.4 to 1.4 mm. in length. In the formal latin diagnosis the achenes are described as "glabris verrucosis," and Plate 799 of the article in Rhodora contains an inset of the glabrous achene and pappus scales. In at least two of the isotypes of this binomial, however, the pappus scales are decidedly acute if not acuminate. Collections made by the author in the same area as the type locality of H. Godfreyi have shown upon examination that not only do both forms of the pappus scale, blunt and acute, occur in the same population but that some specimens had both forms within the same head. Similar collections from nearby counties in South Carolina and North Carolina all show that there is a tendency in these areas toward a blunt and awnless pappus in a number of the specimens. However, such a tendency has been witnessed in other populations of H. flexuosum well away from the Carolina Coastal Plain in Indiana, Missouri and Arkansas. Moreover, the more typical acute and awned pappus scale is encountered in specimens of H. flexuosum quite regularly from North and South Carolina.

Without actually destroying the utility of the type specimen,

a positive statement cannot be made but the author seriously doubts the existence of another glabrous achene within the heads of the type specimen. A few disk florets were removed from each head where it was possible to do so (8 heads in all) and there was not a single glabrous achene among those removed nor were there any in those of the isotypes examined.

Helenium floridanum "concentrated in the northern half of Florida" is distinguished from H. flexuosum according to Fernald by the "ovate pappus pales . . . rounded at tip and terminated by a very long, filiform and smoothish awn . . . [and] in this plant the relatively small heads are either rayless or with well developed ligules." Unfortunately, the pappus scale characters cited as being differential are in no way different from those of the pappus scales of specimens of H. flexuosum from Texas. Illinois, Mississippi, Pennsylvania or Maine. The "relatively small heads" is hardly of any taxonomic importance or descriptive specificity in distinguishing taxa within H. flexuosum proper. The head size is a variable character in this species, seemingly dependent to some degree on environmental conditions, even in the "northern half of Florida." The author suspects that the rayless condition of some of the specimens from Hillsborough and Hernando Counties, Florida prompted the publication of H. floridanum more than anything else. However, this rayless condition cannot be correlated with any other morphological character nor is it constant, there being specimens with some heads rayed and other heads rayless. In addition, the rayless character of some of the specimens of H. flexuosum occurs in other parts of the range of the species, notably Texas.

In this treatment, on the basis of the examination of over 1,500 specimens of *H. flexuosum* from Texas to Maine, no taxonomic recognition in a formal sense is given to *H. Godfreyi* and *H. floridanum* either within or apart from *H. flexuosum* and at most they are considered to represent population differences of relatively small importance within the species as a whole. Viewed throughout its entire geographical range, *H. flexuo um* is a rather variable taxon, especially in relation to the other members of the vernal group of species of *Helenium*. Such variability is not unexpected in a wide-ranging and weedy

species that presumably is not an apomict. The means by which *H. flexuosum* may be distinguished from the other vernal taxa, as well as speculations concerning its origin and history, have been pointed out and suggested in that part of this paper which discusses relationships and there remains no need for repeating them here.—GRAY HERBARIUM, AND ARNOLD ARBORETUM, HARVARD UNIVERSITY.

RANGE EXTENSIONS IN THE GENUS PETERIA (LEGUMINOSAE).¹
—Since the publication of my treatment of the genus Peteria,²
several persons have been kind enough to call my attention to
collections which I had not seen and which extended the range
of two species as mapped in that paper, and to one additional
collection of a third species. In order to amplify the previous
treatment, the following notes are presented.

I am indebted to the following persons for the loan of the specimens cited: Dr. Rimo Bacigalupi, the Jepson Herbarium, University of California (JEPS); Dr. Ray J. Davis, the herbarium of Idaho State College (IDS); and Dr. William H. Baker, herbarium of the University of Idaho (ID).

Peteria Thompsonae S. Wats. This plant is known to have a range extending into southwestern Idaho, Owyhee County: Hot Springs, June 1, 1945, Ripley & Barneby 6511 (IDS); 12 miles south of Bruneau, June 10, 1947, J. H. Christ 16,715 (ID); 13 miles south of Bruneau, June 21, 1956, W. H. Baker 14,023 (ID); Hot Springs Falls, June 27, 1953, Sharp Tisdale, Fosberg, & Helle, s.n. (ID).

Peteria scoparia A. Gray. Known from southwestern Colorado, Montezuma County: Mesa Verde, June 1875, T. S. Brandegee 1103 (JEPS).

Peteria glandulosa (A. Gray) Rydb. An additional collection of this species has been seen: Esperanza, Puebla, Mexico, C. A. Purpus 2474 (JEPS).—C. L. PORTER, UNIV. OF WYO., LARAMIE.

² Rиодова 58: 344-354, 1956.

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